ON THE ASEXUAL ORIGIN OF THE CILIATED SPONGE LARVA.

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IN 1891[1] and in 1894[2] I published certain observations which led me to believe that in monaxonid sponges free-swimming larvæ identical in structure with those developing from eggs are in some species produced asexually. For one such species, *Esperella fibrexilis* Wilson, the observations referred to are in brief as follows: (1) Parenchymal cells well supplied with yolk granules are found collected together in abundant small groups of varying size. Such groups have no definite shape and may contain few cells or many, and the component cells may lie together very loosely or be packed pretty closely.[3] The microscopic pictures indicate that the groups owe their origin to wandering cells that have collected together. (2) Rounded masses of similar cells are found, the cells tightly packed and polygonal in outline. To such masses, which are surrounded by a follicle composed of a single layer of flattened cells, I have applied the term "gemmule." The smaller gemmules are regarded by me as arising from the amorphous masses of parenchymal cells above mentioned, and the microscopic pictures further indicate that the gemmules grow both by cell divisions and by fusion with one another. The gemmules vary greatly in size. The smallest show *in section* only a few cells, the largest several hundred cells,[4] the diameter of the largest gemmules bearing to that of the smallest about the ratio of ten to one. With increasing size of the gemmule, the component

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[1] Notes on the Development of Some Sponges, *Journ. of Morph.*, vol. v, No. 3.

[2] Observations on the Gemmule and Egg Development of Marine Sponges, *Journ. of Morph.*, vol. ix, No. 3.

[3] *Journ. of Morph.*, vol. ix, No. 3, Pl. XIV, Fig. 8; Pl. XV, Figs. 13–15.

[4] *Ibid.*, Pl. XV, Fig. 9, 5 cells; Fig. 16, 18 cells; Fig. 11, 37 cells; Fig. 9, about 60 cells; Fig. 21, about 100 cells; Fig. 18, several hundred cells.

cells are found to be more tightly packed, the fine yolk in the cell bodies is more abundant, and the nuclei are smaller. Hence, to demonstrate cell outlines in the largest (mature) gemmules[1] very thin sections are necessary. (3) Mature gemmules are found in which the compact mass of cells is broken up into a few large masses,[2] on the surface of which are semi-detached single cells, and between and round which lie scattered a few similar free cells. The shape and position of the partially free cells indicate that they are separating as individuals from the subsidiary masses into which the gemmule has broken. Gemmules in this stage are larger than in the mature undivided condition, the spaces between and round the subsidiary masses presumably being filled with absorbed fluid. (4) In other gemmules the subsidiary masses (always irregular in shape and of varying size) are numerous and small, and the free cells are abundant. (5) In yet another stage the constituent cells of the gemmule are found to be completely separated from one another, save that small multinucleate masses continue to be present. The cells of the outermost layer are flattened and form an investing membrane for the inner mass, the cells and multinucleate masses of which are connected together by delicate processes.[3] (6) Transitional stages show that the outer layer of cells becomes the surface epithelium of the larva, which is ciliated except at the posterior pole, while the inner mass becomes histologically differentiated into the several kinds of cells forming the parenchyma of the larva. The larva itself is a typical monaxonid larva, essentially identical in structure with those that are known to develop from segmenting eggs.

Thus an unbroken series of stages is found leading from a small mass composed of a few parenchymal cells to a ciliated larva. The various stages in this gemmule development, including the resulting larvæ, are scattered in great abundance throughout the sponge body, and their presence is associated with degeneration in the structure of the parent sponge. Nowhere in this continuous series of stages is an egg, either undivided or segmenting, interpolated. Very small ova, many times less the diameter of the mature gemmule, are however present, although not common, in the parent parenchyma.

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[1] *Journ. of Morph.*, vol. ix, No. 3, Pl. XV, Fig. 18.

[2] *Ibid.*, Pl. XVI, Fig. 21.

[3] *Ibid.*, Pl. XVI, Fig. 22.

My conclusion that a larva, identical in structure with the typical egg larva of the group, is produced asexually in the manner just indicated has not seemed to certain reviewers (Maas,[1] Minchin[2]) altogether worthy of credence. And it may be that subsequent researches will show that such a conclusion is not necessitated by the facts. What I may point out here, however, is that the conclusion rests upon a series of microscopic pictures, the arrangement of which is left to the intelligence of the observer, and that this is precisely the kind of evidence on which rests our belief that in other sponges an egg development occurs. If, to be sure, the microscopic pictures (images) have been portrayed by me in an inaccurate fashion, then there is no need to consider the logic involved in their arrangement. This is in reality the point of view from which Maas has criticised my account, although he professes to find in my figures evidence for the correctness of his interpretations of them. Maas, in short, very freely and confidently expresses (**'93**, p. 370 ; **'96**, pp. 233–234) the belief that the bodies I figure and describe as gemmules are merely eggs surrounded by masses of nourishing cells ; and that the dissolution of the mature gemmule into subsidiary masses and ultimately into separate cells is only the segmentation of the egg. This process of dissolution specially awakens his incredulity : "Wie man es sich vorstellen soll, und welche Kräfte es bewirken sollen, dass ein Aggregat von Zellen, eine Gemmula, sich in einzelne Stücke weiter und weiter spaltet, darnach will ich hier nicht fragen, sondern nur darnach, warum Wilson in dem ganzen Vorgang nicht eine Furchung, in dem Auseinanderbrechen der Massen in kleine und kleinere Stücke nicht eine Zellteilung gesehen hat ! ?" (**'96**, p. 234). The mechanics of the process to me seem unworthy of so much wonder. Absorption of water by the

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[1] Die Embryonal-Entwicklung und Metamorphose der Cornacuspongien, *Zool. Jahrb.*, Abth. f. Anat. und Ontog., Bd. vii, 1893 ; Erledigte und strittige Fragen der Schwammentwicklung, *Biol. Centralbl.*, Bd. xvi, Nr. 6, 1896.

[2] The Position of Sponges in the Animal Kingdom, *Science Progress*, vol. i, N.S., July, 1897.

mass, coupled with the passage of individual cells from a resting condition, in which mutual pressure gives them a polyhedral shape, into an active condition would appear to be the essential features of the process and are phenomena not altogether outside our experience. Maas has obviously been led astray in his criticism by that well-known condition of mind in which things that are not familiar seem impossible. In a more open and receptive mood he would probably recognize the fundamental differences between the figures of gemmules shown in Pls. XV, XVI of my '94 paper and the figures of Fiedler[1] depicting the growth of the ovum in Spongilla, and would not attempt to explain the former as variations of the latter; more especially when in the same paper (Pls. XXIII, XXIV) I myself represent stages in the growth and segmentation of sponge ova (for Tedanione and Hircinia), the mode of growth in one species (*Hircinia acuta*) closely resembling that of Spongilla as described by Fiedler.

Since the publication of my results in 1894 there have appeared but two communications in which this question is touched upon, on a basis of actual observation. Vosmaer and Pekelharing[2] found in *Esperella ægagropila* certain reproductive bodies of a problematical nature. Not having at the time a sufficiently complete series of stages in the development of these bodies, they do "not enter into the question whether Wilson's statements about *Esperella fibrexilis* are applicable to our sponge." They confirm my observation that the formation of these "gemmules" is associated with degeneration in the structure of the parent sponge, which they find "entirely degenerates and finally dies off." The other communication is from Professor Ijima of Tokyo. This author in his recent beautiful and much admired work on the systematic zoölogy and histology of the Hexactinellida[3] reports observations in the main similar to mine, and is disposed to draw the same conclusion with respect to the origin of the larva. Ijima's observations are as follows :

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[1] Ueber Ei- und Spermabildung bei Spongilla fluviatilis, *Zeitschr. f. wiss. Zool.*, 1888.

[2] Observations on Sponges, *Verhandelingen der Koninklijke Akademie van Wetenschappen te Amsterdam*, 1898.

[3] Studies on the Hexactinellida, Contribution 1, *Journ. Coll. Sci. Imp. Univ., Tokyo, Japan*, vol. xv, 1901.

In *Euplectella marshalli* undifferentiated cells, styled "archæocytes," are found in abundance scattered through the sponge body. Such cells occur "solitarily or in irregular groups of two, three, and so on, up to tens and in certain positions even to hundreds or thousands." The growth of the archæocyte groups "may take place not only by cell division of their cells, but also by fusion of originally separate groups." The smaller groups are flat, the larger ones form solid and compact masses, the shape of which is at first rather irregular. "With continued increase in the number of the cells and consequently in the size of the mass, the latter assumes a roundish, oval or broadly lobose shape, measuring up to 100 μ or more across." Such masses are common in all large individuals. Ijima believes, on the strength of his own and earlier observations, that such congeries of archæocytes are of general occurrence in the Hexactinellida.

In certain archæocyte congeries the cells undergo a histological change, the cell body developing spherules and increasing in size. The transformed cells are known as "thesocytes." The spherules are not firm solids but are of a soft, perhaps even fluid, nature. Ijima concurs in the opinion of F. E. Schulze that the formation of spherules is a metabolic process analogous to the formation of glycogen in liver cells, and that the spherule substance is to be looked on as reserve nutriment. The substance of the spherules is probably of an albuminous nature. Ijima's description of the spherules strongly suggests that the bodies are comparable with the well-known *Glanzkörper* in the rhizopod Pelomyxa (see *Amer. Nat.*, Vol. XXXIV, No. 403).

All the archæocyte congeries are not transformed into thesocyte masses. Of those which are not so transformed, some possibly represent an early stage in spermatogenesis, but Ijima believes that "a good part of the primitive archæocyte congeries are directly and actively concerned in the formation of certain reproductive bodies, asexual or sexual but other than spermatozoa." The further history of such reproductive masses in *Euplectella marshalli* was, however, not followed. But Ijima regards it as probable that similar masses constitute the anlages of the superficial buds known to occur in some hexactinellids (Rhabdocalyptus, Lophocalyx).

In two other species what appears to be the complete intra-parental history of the archæocyte congeries was made out. But before describing Ijima's observations on these forms I wish to digress and point out how much commoner archæocyte masses seem to be in the Hexactinellida than ova and sperm. Ijima recalls the fact that very little is known concerning the ova and spermatozoa of these sponges. Schulze ('80, '87) describes sperm masses and ova (0.3 mm. in diameter) as present in more or less abundance, and usually in the same individual, in *Euplectella aspergillum*. Schulze was never able to discover any distinct segmentation stages. Ijima himself says: "It is somewhat surprising to me that, although the different hexactinellid species histologically studied by me are not few in number, yet scarcely a single case in which either of the sexual products was indisputably developed came under my observation." As regards the male elements Ijima says he is quite in the dark, that he has never seen spermatozoa or indisputable sperm masses, nor indeed does he feel disposed to say that he has seen ova. In one specimen of *Euplectella marshalli* a number of cells were observed, the larger ones measuring 10–15 μ, sometimes 23 μ, in diameter. Such cells are connected by transitional stages with, and are undoubtedly derived from, archæocytes. Ijima thinks these cells are young stages in the development of bodies similar to those described by Schulze as ova in *Euplectella aspergillum*, but does not commit himself to the view that they are eggs. In another sponge, a specimen of Leucopsacus, comparatively large spherical or ovoid cells, 20–40 μ in diameter, were found in some abundance. Such cells were not connected by transitional stages with archæocytes, and the describer again does not find the evidence for their ovum nature absolutely convincing. The fact that Ijima found no indubitable sexual elements is the more surprising since in the case of *Euplectella marshalli* he made special search for them, examining numerous specimens collected during the four seasons of the year. The rarity of these elements suggests that the sexual breeding season of the Hexactinellida, *if it occurs annually*, is one of very short duration.

In the two species above alluded to, *Leucopsacus orthodocus* and *Vitrollula fertile*, Ijima has discovered not only archæocyte masses but also larvæ, the only hexactinellidan larvæ as yet observed. Reserving for a later contribution his detailed observations on these bodies, Ijima contents himself for the present with a sketch of their structure and development. The larvæ are spindle shaped, thicker at one end, and consist of a superficial flagellated layer covering an internal mass of cells. The hexactinellidan larva is thus fundamentally similar to that of monaxonid sponges. In an earlier stage the embryo is spherical in shape, with no discernible flagellation, and consists of a compact mass of small cells, those of the superficial layer showing an epithelium-like arrangement but not differing in general appearance from the internal cells. "At a still earlier stage there is found a simple cellular mass agreeing in all respects with the latter" (the stage just described) "except in having no distinct epithelial covering. And that simple cellular mass is in all appearance nothing else than an advanced stage of what I have called the archæocyte congeries, of which there exists a series of different sizes, leading down uninterruptedly to the little groups of cells so commonly found on the chambers. At all events, there is nothing else than these compact groups of small cells to which the origin of the developing embryo can be traced back with any degree of probability."

Ijima appreciates the remarkable character of the development just sketched and, before definitely formulating an opinion as to the asexual origin of the larva, wishes to continue his observations on a more plentiful supply of material than he has hitherto had. His position is best stated in his own words: "To repeat, to me it seems certain that the embryo in a very early stage of its development consists of a small assemblage of uniform-looking cells, which differ in no distinguishable feature from the archæocytes. If the resulting body were something comparable to a bud or gemmula, I would probably have felt no hesitation in concluding that the cells were really archæocytes, and that we had here to do with a case of asexual reproduction. But, free-swimming larvæ, essentially similar to those developed from ova in other sponges, being at issue, the question whether true ova are not somehow complicated in the cell mass whence the larva arises seems to claim to be brought on the tapis, all the more, since our knowledge of the hexactinellidan ovum is far from being satisfactory." And again, p. 188, after mentioning my observations and conclusion, "I conceive the mode of origin and growth of the archæocyte congeries in the Hexactinellida to be just the same, and it seems to me not impossible that in the hexactinellid larvæ which I have seen we have simply a new case of the 'gemmule larva' or bud embryo." After referring to Maas's view that my conclusion rests upon a mistaken interpretation of a process of oögenesis, Ijima goes on to say with regard to his own observations, p. 189: "So far as concerns the archæocyte congeries of the Hexactinellida, I can confidently state that among the constituent cells in any stage of its growth, there exists not one which, on account of its size or of other external peculiarities, can be recognized as an egg. If it be that so many cells are aggregated for the sake of the nutrition of a developing ovum, this ovum is to be expected to deviate more or less morphologically from the rest as it approaches maturity; however, no sign of such a differentiation is noticeable. Further, all the cells in a congeries, large or small, are tolerably uniformly and compactly packed together, so as to directly touch one another; and where they are somewhat loosely arranged, there is not a trace of any substance between them. So that I am decidedly against the assumption that some of them are, at any stage of the growth of the congeries, engulfed among certain others as pabulum. If, after all that, a portion or all of the cells in a congeries giving rise to an embryo are still to be looked at in the light of blastomeres that have arisen by segmentation from a single egg cell, one is driven to the assumption that the original ovum is, like the blastomeres themselves, as small-bodied as, and indistinguishable from, an archæocyte. This would be very remarkable in an ovum; and moreover, under that supposition, it becomes imperative to deny egg nature to the large ovum-like cells described by Schulze and by myself from Euplectella." Such an hypothetical mother cell of an embryo as Ijima suggests in the above excerpt would be something so different from an ovum that to class it as such, it seems to me, would be to confuse our ideas concerning reproductive cells. It would rather be analogous to a spore. However, both Ijima's observations and my own on the character of the smaller groups of archæocytes and their growth by fusion render unwarranted the assumption that any such cell exists, that is, as a typical and necessary condition in the development of an embryo. That a single cell may occasionally and incidentally give rise to a gemmule and so to an embryo is, of course, a possibility. And thinking over the possibility of such a case tends to clear up our ideas as to the nature of the typical reproductive archæocyte which acts in coöperation with others to form a new individual. If the hypothetical, exceptional archæocyte, which independently produces an embryo, is to be looked on as equivalent to a spore, the same view must be entertained regarding the typical coöperative archæocyte. In the one case we have a single spore producing the individual, while in the other case several spores unite, as, for instance, in the production of a myxomycete plasmodium (sporangium). Into the deeper-lying question as to how fundamental is the difference between an ovum and a spore there is no need to go. That there are, except in some of the plants, certain great and obvious differences no one will deny.

From a theoretical standpoint further investigations of this type of development in the sponges are much to be desired, and Professor Ijima's contribution will scarcely fail to call them out.

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